

27. HUMAN EXPERIENCE OF THE TASTE AND SMELL OF INSECTS AFFORDS UNTRUSTWORTHY EVIDENCE OF THE EFFECT UPON THE SENSES OF INSECTIVOROUS ANIMALS. (E. B. P.)

The idea that human experience would supply a valuable test as to the palatability or unpalatability of insects to their natural foes has occurred to more than one naturalist. In Section 7 of his paper (Mém. de la Soc. Zool. de France, tome vii, 1894, p. 375, § 7), Professor Félix Plateau describes what he calls the "real taste" ("savour réelle") of the larva, pupa, and imago of *Abraaxas grossulariata*: meaning by the words "real taste" the impression produced upon his own palate. After some natural hesitation he tasted a fine lively specimen of the larva, first cutting it transversely into two pieces. After masticating it sufficiently long to be sure of the impression produced, he affirms that it is almost without taste, very slightly sweetish, with nothing whatever unpleasant about it: "ni nauséabonde, ni poivrée, ni acide, ni amère, sans arrière-goût, et j'ajouterai même *agréable*, rappelant un peu celle des amandes douces sèches ou de la noix de coco." The skin is however somewhat tough, which Plateau suggests as a possible reason for the rejection of the larva by certain vertebrate enemies. The pupa was very similar, but even more tasteless than the larva; while the abdomen of the moth produced much the same effect when masticated: "la saveur m'a paru faible, *agréable* et analogue à celle de la chenille."

Plateau considers his experience to be entirely convincing and decisive as to the real taste of the insect to all insectivorous animals. But it is perfectly obvious that the only point which has been proved is that *a single individual of an animal not habitually insectivorous has found this insect to be rather pleasant in taste although decidedly insipid*. But this fact does not enable us to judge in any way of the impressions produced upon the senses of a truly insectivorous animal. That evidence must be judged upon its own merits, and, as Plateau appears to consider that he has shaken it, I give a somewhat detailed account of his treatment of the subject, and especially of his own valuable and interesting experiments, some of which were conducted upon insect-enemies hitherto unobserved and untried from this point of view. In view of the far-reaching character of Plateau's conclusion it becomes necessary to re-examine the

whole of the evidence for the unpalatability of *Abraxas grossulariata*, especially the larva, which has been chiefly employed for the purposes of experiment. Professor Plateau gives a fair and admirable résumé of the work of the earlier experimenters on the larva, showing that they arrived at the opinion that it was unpalatable, from the uniform behaviour of many European insectivorous animals, viz. many species of birds,\* two species of spiders, the common frog, the tree frog, and many species of lizards. In describing the last experiments, those of F. E. Beddard, F.R.S., and F. Finn, conducted almost exclusively upon non-European animals ("Animal Coloration," London, 1892, pp. 149, 164, 165), the conclusion is omitted: "these experiments show that, with a few exceptions, the caterpillar of the magpie moth is distasteful to animals." Although a marmoset "ate one up quite greedily," the behaviour of two *Cebus* monkeys and a *Cercopithecus callitrichus*, as described by Mr. Beddard, is most suggestive of the errors likely to arise from a too-exclusive study of insectivorous animals able in confinement to eat but little, or nothing at all, of a food they would obtain in the wild state in plenty and variety. These monkeys "sucked at the caterpillar and threw away the skin after the contents had been entirely extracted; they paused every now and again to sniff suspiciously at the caterpillar, but nevertheless they steadily persevered in munching it." Mr. Beddard's account of the behaviour of non-European birds entirely confirms the conclusions derived from a study of European insect-eaters. It is probably safe to conclude that the species had never seen the larva before, and it is not surprising that many of them should peck at it. But although from Mr. Beddard's statement (*loc. cit.* p. 149) it is clear that over a dozen species were experimented upon, the only bird which certainly swallowed the larva was a large ground cuckoo (*Carpococcyx radiatus*). The author

\* I am now glad to be able to add the evidence that a sparrow in the wild state rejected this moth after capturing it. The observation was made by my friend Mr. G. C. Griffiths, F.E.S., of Clifton, Bristol, a naturalist of great experience and powers of observation. Mr. Griffiths writes as follows:—"I was standing on June 30, 1900, among the trees on Clifton Down at mid-day, when a specimen of *A. grossulariata* flew out from a wych-elm and passed slowly across over a gravel path. A sparrow darted after it and bit off all its wings, but held its body scarcely an instant, dropping it upon the path, where I picked it up—a very satisfactory proof of its distastefulness."

is also "inclined to think" that a white-eye (*Zosterops*) ended by swallowing the insect after masticating it for a long time. The behaviour of the cuckoo is really confirmatory of previous observations, for it has been long known that our own cuckoo is a coarse feeder, and there is even evidence that it eats this very species, as pointed out by our President in the Annual Address for the present year (Proc. 1901, p. xli). The experiments made by Beddard and Finn on lizards support previous conclusions: "chewed and refused by *L. viridis*, and disregarded by *Zonurus* and *Amphibolurus*;" but they state that a toad ate the larva. From their other observations on these Amphibia, it appears certain that toads are indifferent to modes of defence which are efficacious against the majority of insect-eaters; but many more observations and experiments under various conditions are needed before we can safely conclude that *Abraxas* is palatable to these enemies. As possessing some bearing on the question, it is to be noted that a toad which had swallowed a caterpillar of *Euchelia jacobææ*, "almost immediately threw it up" (p. 159).

We now come to the more recent experiments of Professor Plateau. He found (§ 5) that eight *Cistudo europæa*, which were certainly insectivorous, inasmuch as they devoured beetles, paid no attention to the larva of *Abraxas*, with the exception of one individual which seized a larva and then abandoned it. *Coluber esculapii* and an Italian variety of *Lacerta muralis* paid no attention to them, and if, when one of them opened its mouth, a larva was inserted, it was immediately rejected. As regards Amphibia (§ 6), Professor Plateau found that the common frog acted exactly as Dr. A. G. Butler has described. He further believes that the frog never again attacks the caterpillar which it has once seized and rejected, although, as the larva walks off quite uninjured, the frog sometimes follows its movements for a few seconds. He then threw some larvæ into an aquarium containing a number of *Triton punctatus*, many of which seized and "made efforts to swallow them, giving, according to their custom, sharp blows with the head to right and left. But the prey was too big, or the skin too tough, for the Tritons abandoned them after a few minutes." The newt swallows its prey whole, and has great powers of expansion to meet the special difficulty of size, so it is far more probable that these Amphibia were influenced in the same manner as

the frogs and the water tortoises experimented on by Professor Plateau. He then offered the larvæ to the larger *Triton alpestris*, which paid no attention to them.

Professor Plateau's experiments on spiders are described on pp. 325-7, where it will be seen that the larvæ were either neglected or treated as A. G. Butler described by *Amaurobius ferox*, *Tegenaria domestica*, and *Agelena labyrinthica*. The imago on the other hand was constantly eaten by *Tegenaria*, offered once to *Epeira diadema* and eaten with avidity, killed but rejected by *Agelena*.

His experiments on *Carabus auratus* and two species of *Dytiscus* are described on p. 330: they indicate clearly that these predaceous beetles freely attack and devour both larva and imago of *Abraxas*.

The above is a résumé of the evidence as Plateau gives it, although he also includes the attacks of insect-parasites. These I have quoted on p. 338; but the other observations recorded in the same section of this memoir indicate that insects with warning colours and distasteful to the (non-parasitic) enemies of their class are specially liable to these attacks, so that the results obtained by Plateau in this section (§ 10) of his paper tend, so far as they go, to support the conclusions he seeks to destroy.

As regards the vertebrate enemies Plateau has supplied a considerable amount of evidence in support of the conclusions of his predecessors. He shows that certain spiders are probably, and some predaceous beetles almost certainly, enemies of *Abraxas* in one or more stages. These latter facts are most interesting and valuable, but they no more controvert or throw doubt upon the behaviour of the generality of insectivorous vertebrates than the admitted exception of the cuckoo, and the pleasant impression produced upon the Professor himself. All the theory of aposematic colouring requires is that the conspicuous form should be unfit as food for the majority of the enemies of its class; and this has been abundantly proved in the case of *Abraxas*. It is unimportant whether our anthropomorphic terms unpalatability, distastefulness, etc., truly express what an animal feels, if we admit the fact, as we are bound to do after the experiments, that the majority of insect-eaters after trial do not eat the insect, and after one or more trials do not seek to eat it unless driven by starvation. Exactly what impressions they feel we can never know, and it is quite unnecessary for the theory

of warning or aposematic coloration that we should know. The behaviour is sufficient, and affords convincing proof.

Plateau also brings two indirect lines of argument to bear on the question. He points out (§ 3) that the larva is not wholly conspicuous, but requires searching for if it is to be obtained in large numbers. This is due to its habit when young of resting along the serrated edges of leaves, exposing only the reddish lateral band sprinkled with black points. This appearance is at a little distance very like the reddish edges of many leaves. When it is older he observes that it stretches itself longitudinally along the branches in the inner darker part of the bush at no great height above the ground. When the bush is shaken it falls or lets itself down by a thread; and as soon as it reaches the ground rolls in a ring. In this position, which it retains for a long time, it resembles the excrement of a bird. Mr. Beddard too points out (*loc. cit.*, pp. 167, 168) that these larvæ "like other Geometers . . . do not begin to feed until evening. I have a quantity of these caterpillars on some thick-leaved shrubs in my garden; during the daytime none are visible, but in the evening they commence to crawl about quite actively." I have myself often observed the larva moving and freely exposed by day on the sides and tops of hedges, but after the statements of these two naturalists I am quite ready to believe that my observations were exceptional. Indeed on general grounds I must believe that this is so; for it would not be an advantage but a great disadvantage to the *Abraxas* to display its aposematic colouring at too great a distance. It has certain enemies, such as the cuckoo, and it would doubtless be dangerous if these were able to see it upon the bush at a great distance. Its colours would be conspicuous enough to the majority of insect enemies hunting the bush for food; and the *very* rough resemblance to leaf-edges, branches, and birds' excrement would never impose upon the eyes which enable their owners to find abundant food in spite of the extraordinarily close likeness to each one of these objects which is attained by so many of the cryptic species which they hunt.

Plateau's second indirect argument depends on the undoubted fact that the pupa of the *Abraxas* resembles a wasp. This he regards as an example of (Batesian) mimicry, and believes moreover that it has never been pointed out before. This is very far from being the case.

In my paper "The Experimental Proof of the Protective Value of Colour and Markings in Insects in Reference to their Vertebrate Enemies," Proc. Zool. Soc., 1887, p. 191, I published a Table (A) of the various combinations of colours of conspicuous insects. Section III of Table A, on pp. 232, 233, contained the combinations of black and yellow and of yellow and black; under the former was placed the pupa of *Abraas grossulariata* and several Hymenoptera Aculeata, etc., under the latter the larva of *Euchelia jacobaeae* and other species. Another Table (B) grouped conspicuous insects according to their patterns. Section I of Table B, on p. 236, is as follows:—

I.—*Ring Pattern.*

Pattern developed on abdominal segments.	{	Pupa of <i>A. grossulariata</i> .	{	Alternating rings of yellow and black.
Developed on whole length of body.		Imago of <i>Vespa</i> , <i>Nomada</i> , and <i>Bombus</i> .		

The following sentences refer to this very section of Table B:—"There is probably in some cases a certain amount of true mimicry in the acquisition of patterns and colours. Thus it is more than probable (as has been previously suggested by other observers) that the species rendered conspicuous by alternate rings of black and yellow gain great advantages from the justly respected appearance of hornets and wasps. It must not be forgotten, however, that the latter forms also probably gain to some extent by the greater publicity which follows from the resemblance" (pp. 235, 238). Furthermore in 1890 the same conclusions were re-stated in almost the same words, save that the species indicated in Table B, Section I, are here introduced into the text:—"Thus it is more than probable that the species marked by alternate rings of black and yellow (including the chrysalis of the Magpie Moth and the caterpillar of the Cinnabar Moth) gain considerable advantages, etc." ("Colours of Animals," London, p. 186).

It is hardly necessary to point out that the resemblance to a wasp is no evidence of palatability, any more than the resemblance, which is often strongly marked, in the same district between wasps of different genera and between



them and Hymenoptera Aculeata of other sections. The present memoir contains splendid examples of Müllerian or synaposematic associations between inedible forms such as *Lycidæ* and stinging Aculeates (see p. 517), and the resemblance between *Abrasus* and a wasp is probably of the same kind, as I suggested in 1887.

My friend Professor W. M. Wheeler of the University of Texas has also tasted a Syrphid fly, *Spilomyia fusca* (Loew), which mimics *Vespa maculata* as well as a smaller wasp. The fly was "found to have an agreeable flavour, the alimentary tract of the insect being full of honey." Hence in this case Professor Wheeler concludes that the colours of the fly are "associated with the absence of disagreeable smell and taste, as the generally accepted theory of mimicry requires" ("Science," N. S. vol. vi, No. 154, p. 887, Dec. 10, 1897). Still later in "The Century Magazine" for July 1901, p. 378, Professor Wheeler describes another experiment as follows:—"The writer while riding through the deserts of Wyoming some years ago was impressed with the day-flying moths (*Pseudohazis*) flitting leisurely along near the ground or resting fully exposed on the glaucous spikes of the sage-brush. . . . They had black-and-white wings and black-and-orange bodies. So striking was this case of apparent warning colour that the writer after much hesitation decided to ascertain by means of the only available experiment whether the insect really possessed the 'nauseous properties' so generally assumed in such cases by writers on the subject of animal coloration. He dismounted from his horse and proceeded to masticate the body of one of the moths. To his astonishment, the little flavour that it contained was mild and pleasant—one might almost say, nut-like." The writer also records that lizards previously fed on house-flies, and therefore not very hungry, "devoured with evident signs of relish" several of the conspicuous day-flying moths *Alypia octomaculata*. Professor Wheeler concludes "that if every field-entomologist could only bring himself to repeat the writer's experiment on *one* of many cases of 'flaunted nauseousness,' and place his taste-impressions on record, we should in the course of time have a really valuable body of evidence, for we can hardly assume that beasts, birds, and reptiles can find things 'nauseous' which are quite tasteless or even pleasant to the human palate."

I believe, on the contrary, that we are justified in the opinion expressed in the last words quoted from Professor Wheeler, and I have proved that we have very good grounds for maintaining that a conspicuous insect pleasant to the human taste is rejected with probable signs of disapproval by many truly insectivorous animals. The tasting of conspicuously coloured insects by entomologists in general, recommended by Professor Wheeler, would I believe be of very little value or more probably of no value at all as evidence of the likes and dislikes of insect-eating animals. Carefully conducted experiments upon such animals, and still better observation of them and their prey in the field, and the examination of the contents of their digestive canal and the components of their faeces, are the only means by which trustworthy conclusions can be reached. We have to deal with a heterogeneous group of animals, alike in one respect, viz. the specialization of digestive apparatus and sense-organs to an insect diet. It is reasonable to suppose that, whatever we may find in man and other forms not markedly insectivorous, in the members of this particular group there will be a specially acute sensitiveness to qualitative differences amongst the innumerable species from which they select their food. It is probable that especial keenness for certain species indicates a high nutritive value, and that the sense-organs of insectivorous animals enable them to detect and thus to reject species which would have an injurious effect, or at the least would be of comparatively low value as food. There is no reason for the belief that an equal degree of specialization exists in animals which are not insectivorous. Least of all is this likely to be the case in man, with his comparatively minute olfactory lobes, the central organ by which there is appreciation of every kind of flavour as well as every variety of scent.

I have thought it desirable to argue the question at some length, inasmuch as the two distinguished naturalists I have quoted, as well as others, find significance in human experience of the taste of insects. The opposite conclusion has always seemed to me inevitable from the considerations set forth above; but if any doubt remains it must be dispelled by reading the following account of Mr. Marshall's experiments upon himself, and comparing it with those which he conducted upon insect-eating animals of many kinds. It is interesting that he should detect bitterness,



acridity, and a Coccinellid-like smell in certain species, but even in these the human experience is probably very faint compared to that of a truly insectivorous animal. Nor does it by any means follow that a scent which is excessively unpleasant to man indicates unpalatability to all or even the majority of natural foes, as in the obvious case of *Anoplocnemis curripes*, the evil-smelling Coreid bug eaten greedily by baboons (see p. 382), although rejected after tasting by a kestrel (p. 345). Professor Plateau and Professor Wheeler will probably reconsider the significance of their own sense-impressions when they read below that Mr. Marshall could detect nothing unpleasant in the much-mimicked *Limnas chrysippus*.

"*Estcourt*, Oct. 15, 1896.—I have for some time intended to make experiments on the taste of the *Acræas*. . . . However, my tasting experiments have not helped me much, for my sense of taste is evidently not as acute as that of birds and lizards. However, I send you the few notes I have made in case they may be of interest or use.

"In *Acræa nohara*, *buxtoni*, *cabira*, and *Planema esebria*, I was unable to detect any trace of bitterness or acridity, and they appeared to me quite insipid; indeed, as far as mere taste is concerned, I doubt whether I could distinguish them from *Belenois severina*, though their outer integuments are much tougher. [Mr. Marshall subsequently found that *buxtoni* does possess a bitter juice, which exudes freely from the wings when they are cut, especially at the bases.] This alone is sufficient to prove the unreliability of the test, for *cabira* is most certainly an inedible species, even if *esebria* is doubtful. *A. encedon* and its var. *lycia* exude a yellow juice from the thorax which is slightly bitter, but not very markedly so. *Acræa anacreon* and *natalica* both exude juice in the same manner, but it seems distinctly more bitter than that of *encedon*. *A. ancmosa* in addition to the bitter juice emits a very strong smell when pinched, being the only *Acræa* in which I have noticed this, though possibly *acara* does the same, as I regard these as the two best-protected members of the genus. *Planema aganice* has no smell, but emits a lot of acrid juice, not only from the thorax, but also from the antennæ and the nervules of the hindwings. With regard to the juice-exuding species I may note that the bitter taste appears to lie only in the exudation and not to permeate the tissues of the body.

"In the few specimens of *Amauris echeria* that I tried I found that no juice was emitted, but they had a nauseous taste and a strong smell, which reminded me somewhat of that emitted by many *Coccinellidæ*. But it was *L. chrysippus* which showed me the futility of trying to arrive at any definite conclusions from this line of research, for it emits neither juice nor smell, and I could detect no trace of any taste, unpalatable or otherwise, but the tissues have a somewhat soapy feel to the tongue, which I noticed in *A. echeria* and some of the *Acræas*. The same may be said of *Mylothris agathina*, though from its conspicuous colouring, slow flight, and wide dispersal, I feel sure it is an inedible species.

"*Malvern, Feb. 21, 1897.*—*Acræa horta* exudes a bitter yellow juice from the thorax when it is injured, and this juice permeates the costa of the fore-wing. The head and abdomen do not appear to me to have any unpleasant taste. Trimen refers to their smell, but my smelling powers are not sufficiently acute to detect it.

"*Malvern, May 14, 1897.*—*Alena amazoula* feigns death most persistently; it has an unpleasant taste and strong smell not unlike that of the *Coccinellidæ*."

## 28. GUY A. K. MARSHALL'S PROOF OF SEASONAL CHANGES IN SOUTH AFRICAN BUTTERFLIES OF THE GENUS *Precis*. (E. B. P.)

### A. Introduction.

The attempt will be made in the following section of this memoir to explain these astonishing changes as due to the adaptation of a moderately distasteful and protected genus in two directions—towards conspicuous warning colours in the generations of the wet season, the time when insect-food is abundant; towards procryptic concealment in the pressure and scarcity of the dry season.

Facts which require for their interpretation the hypothesis of adaptation in the direction of conspicuousness will be brought forward, much use being made of the conclusive proof only recently obtained by Mr. Marshall, by breeding the one from the other, that *Precis simia* is the wet phase of *P. antilope*.

The distinct habits and stations of the two phases, their relation to other seasonal forms of butterflies, the observed